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THE DEVELOPMENTAL CYCLE OF ELAPHO-
STRONGYLUS RANGIFERI MIZ., 1958
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In the study of elaphostrongylosis in deer (*Rangifer tarandi*), the pathogen of this disease was identified as *Elaphostrongylus rangiferi*, a nematode of the Protostrongylidae (Mitskevich, 1959). The sexually mature stage parasitizes in the deer brain (under the pia mater membrane in convolutions of the large hemispheres) and in muscular connective tissue. The associated intermediate hosts of *E. rangiferi* are various shell-bearing terrestrial and freshwater mollusks (Mitskevich, 1958, 1960, 1963).

The results of the following research are described:

- 1) on the survival in external media of first-stage elaphostrongyl larvae,
- 2) on the development of larvae within the intermediate hosts, and
- 3) on the length of development periods of elaphostrongyls in the organism of the definitive host.

Survival of first-stage larvae in artificial medium

Initial material in these experiments were first-stage larvae obtained by Berman's method from feces of deer, periodically supplied by reindeer farms and zoological gardens.

The experiments and observations were carried out on the effect on first-stage larvae of drying, moisture, low temperatures (including prolonged freezing), high temperature and direct solar radiation. Survival of larvae under laboratory and natural conditions was followed as well.

The effect of drying. First-stage larvae were placed on glass slides framed in Canada balsam (to prevent loss of larvae) and counted. The slides were left open until completely dry. They were then wrapped in paper and examined at fixed intervals, from the first day up to one year. On the expiration of a predetermined period the slides were moistened with water; 16 to 20 hours later the number of living larvae were counted. Material was either dried once or several times (after moistening as described above).

On single drying 100% of the larvae survived up to 5 days. Non-motile and dead larvae first appeared after 6 days. The last signs of motility (8-9%) were observed after 30 days' drying. On subsequent days, larvae remained

alive but were non-motile; such larvae (up to 40%) could be seen after 330 days of drying; only after 340 days were all the larvae found to be dead.

Repeated dryings were carried out at intervals of 5, 10, 15 and 30 days. In every 5 days' drying, motile larvae could be detected after 30 days, that is, after 6 dryings. Dead larvae appeared after the first drying, after 6 to 10 days. Non-motile[sic] larvae disappeared after 9 to 30 drying exposures, which is equivalent to 1.5 to 5 months. A few solitary living larvae were occasionally observed after 47 days.

In dryings at 10-day intervals, live larvae were still seen after three such exposures, i.e., after 30 days. Dead larvae were detected after the first exposure (10 days). As a rule, live, non-motile larvae are detected for up to 4 months, exceptionally up to 7 months; that is, they withstood from 12 to 21 dryings.

Where the exposures to drying were at 15-day intervals, live larvae were observed as in the two preceding experiments for a period of up to 15 to 30 days, or after one or two drying exposures; dead larvae appeared after the first exposure, and non-motile larvae disappeared after 2 to 3 months.

In drying exposures every 30 days, small numbers of motile larvae (8.9%) were observed after the first exposure, as in the case of a single exposure. Larvae remained viable in the non-motile state for up to 390 days (13 exposures), but after 9 exposures to drying (after 270 days) mass death occurred.

It follows, then, that drying combined with periodical moistening shortens the life-span of larvae. However, during the first 30 days such treatment has no effect on larvae. When moistened at greater intervals, dead larvae appear sooner. In all drying experiments on larvae taken from feces, material taken in winter showed more rapid mortality than the experimental material initiated in autumn.

It appears, therefore, that first-stage larvae have great resistance to both single and repeated dryings.

Effect of moisture. Motile first-stage larvae were placed in test-tubes or containers with a layer of water 8, 3, and 1 cm in height. The water over the larvae was changed every 5 or 10 days (during the test for larval motility). The larvae were introduced in July, August/September, December, and February. Some containers were kept in constant-temperature rooms of 15°C and 20°C for one year, while others were left out-of-doors.

The condition and behavior of larvae after one hour under 8 cm of water, both in constant temperature and out-of-doors, showed no changes.

Larvae survive in moisture at various temperatures for a long period of time. When introduced in August/September, they survive in laboratory conditions for 11 months, and out-of-doors for 9 months. Until December such larvae are very motile; subsequently they remain non-motile for 4 to 5 months in a state of anabiosis, and at the end of March, beginning of April, show renewed mobility and are capable of infecting intermediate hosts. Mass deaths begin in August. In the experiment begun in December, the larval life-span did not exceed three months, after which mass destruction of larvae occurs. Larvae introduced into the experiment in February remain alive indoors for 7 months, and for 4 months out-of-doors.

Such larvae are motile and do not exhibit anabiosis, but their movements are sluggish, and the percentage of survival is very low (2 to 3%).

The July larvae live for 11 months under laboratory conditions and for 12 months in natural conditions; they perish in masses at the end of this period. As in the September batch, anabiosis occurs from December to April. This behavior pattern was observed in larvae kept all the year in water at room temperature and in larvae placed in natural conditions exposed to direct solar radiation as well as prolonged freezing.

Larvae kept in water at a depth of 3 cm remain alive for shorter periods in both natural and laboratory conditions. The summer and autumn batches of larvae remained viable in the laboratory for 9 months, without passing in winter into a state of immobility (as observed in the first experiment). Larvae kept in natural conditions retained vitality for 10 months. From the end of December until the beginning of May such larvae were in a state of immobility. The February larvae survived 3 months at room temperature, and from 4 to 5 months under natural conditions.

Larvae immersed at the depth of 1 cm (both the late summer/autumn and February batches) survived under natural conditions for 3 months. The former lot perished at the end of December, and the latter at the end of May. On the other hand, laboratory-kept larvae introduced into the experiment in August/September perished after 3.5 months, while the February batch remained alive for 8 months.

Water, then, is a beneficial factor favoring, at all seasons of the year, the survival of larvae. The height of the water over the larvae seems to affect their life span.

Effect of low temperature (freezing). In January and February larvae were placed on glass slides for dry freezing, and in weighing bottles for freezing in water (under 1 to 3 cm of water). They were kept in a refrigerator or out-of-doors, and at specified times the larvae were examined. Material was frozen both once and repeatedly, after thawing, from the first day's freezing up to six months. To determine larval motility after thawing, observations were performed after the warm season had begun.

Results show that the larvae survive dry freezing for a period up to 2—3 months only; mass deaths ensue at the end of March or in April, and occasionally early in May. Retention of motility of larvae was not affected by alternate thawing and freezing. Larvae subjected to freezing in water retain vitality longer. For instance, after initial freezing in water in January, larvae remained motile until the end of April; when frozen in February, vitality was retained until August, whereupon mass mortality was observed. Larvae frozen throughout the whole winter (6 months), during which they appeared dead, became motile only after thawing in March, and remained active until July/August.

Larvae which had remained in an external medium since autumn showed a most vigorous power to persist. The winter larvae, excreted by animals in December and January, as a rule perish in April. Repeated freezing and thawing of larvae during the winter, autumn and spring does not affect their vitality, as is observed in other strongylate representatives (*Dictyocaulus*, *Trichostrongylus*). Thus larvae periodically thawed and again subjected to freezing every 5 to 10 days retained their vitality until

July or August, whereas those subjected to periodic thawing and freezing every 15, 20, 25 and 30 days as a rule perished by April; only an insignificant number remained motile as late as June.

It follows that first-stage larvae were very resistant both to single and to repeated freezing.

Effect of high temperature. Larvae were immersed in water in test-tubes and heated up to 50°C—60°C. Test-tubes were incubated in a water bath at these elevated temperatures for from 5 to 60 minutes. After cooling, the material was examined for larval motility after 1, 24 and 48 hours. Even after a short heating of 5 min at 50°C, larvae were killed. After an hour, only 8% of the larvae were motile, while after standing for 24 hours 3% were motile and after 48 hours only 1%. More prolonged heating (of 24 hours and 48 hours) completely destroyed the larvae.

Therefore, it can be seen from these results that high temperatures destroy first-stage larvae.

Action of direct solar radiation. Larvae were placed on dry glass slides as well as on slides with a thin layer of water, within Canada balsam frames, and placed out in the sun. Slides were exposed for periods of from 5 min to 3 hrs and even longer. The slides were then examined under the microscope for motility of larvae, 5 min, half-hour, 1, 3, 24 and 48 hours after exposure. In some series of experiments, the heating effect of solar radiation was neutralized. All larvae kept moist were found to be motile right after exposure to solar radiation of up to 3 hours and longer. Dry larvae withstood exposure for 1 hour, 97% of them becoming active en masse 24 hours later. Three-hour exposure to solar radiation resulted in from 7% to 100% survival of larvae, when observed 24 to 48 hours after exposure. In the experiments in which heating effect was removed, larvae invariably collected near the edge of the glass, their behavior in other respects being similar to that of larvae in the other series of experiments.

Therefore, the action of direct solar radiation is withstood well by larvae; this especially in natural conditions on pastures, where they are nearly always in a moist medium.

Duration of larva's life in fecal masses. To ascertain the length of the larva's survival in fecal masses, such masses were placed in boxes in pastures, as well as in the laboratory. The boxes each contained 12 compartments, in which excrement of elaphostrongylosis-infected deer was placed. Some boxes kept on pastures were left in exposed places, others in a shed. During a period of almost three years the feces were examined every 5 or 10 days.

These observations have shown that the larvae in feces remain alive over two years under all conditions, whether in the laboratory or in natural conditions, in open pasture or in a shed. The duration of survival fluctuated with the degree of drying, but even in the most unfavorable conditions (complete indoor drying) larvae survive for 270 days. In feces subjected to freezing and thawing on the pastures, where they were exposed to solar radiation and to rains, living larvae were found after 27 months. The number of larvae in boxes kept in the shed was usually greater, but no differences were observed in the duration of survival. During the first year, every sample examined contained large numbers of larvae. Afterwards numbers began to decrease, and after 27 months'

exposure only few motile larvae were encountered on examination. Further observations were not pursued. On the average 10% of the larvae survive the winter. No vertical migration of the first-stage larvae could be detected in the material; they are washed out of the feces only by water. With the drying-up of fecal masses larvae move rather actively onto the surface strata of the earth. In spite of their durability, first-stage larvae neither grow nor undergo morphological changes.

The foregoing observations indicate that first-stage larvae, being very resistant to a vast variety of unfavorable external influences, are capable of surviving in nature for over a year. They live through the winter and the dry season and accumulate on the pasture, in greater numbers in water, where constant infection of intermediate hosts is ensured.

Development of elaphostrongyl larvae within the intermediate hosts

In our experiments terrestrial and freshwater mollusks were subjected to infestation.

THE TERRESTRIAL MOLLUSKS WERE:

1. *Trichia hispida* (L., 1758).
2. *Zenobiella rubiginosa* (A. Schm., 1853).
3. *Succinea putris* (L., 1758).
4. *Eulota fruticum* (Müll., 1774).
5. *Euconulus fulvus* (Müll., 1774).
6. *Zonitoides nitidus* (Müll., 1774).
7. *Helix lucorum* (L., 1758), sent in considerable quantities from Azerbaidzhan.
8. *Agriolimax agrestis* (L., 1758).
9. *A. reticulatus* (Müll., 1774).

THE FRESHWATER MOLLUSKS WERE:

1. *Limnea stagnalis* (L., 1758).
2. *Radix auricularia* (L., 1758).
3. *R. ovata* (Draparnaud, 1895).
4. *R. peregra* (Müll., 1774).
5. *Galba palustris* (Müll., 1774).
6. *G. truncatula* (Müll., 1774).
7. *Coretus corneus* (L., 1758).

Of the terrestrial mollusks, the most intensively infested were *Trichia hispida* and *Succinea putris*, and of the freshwater mollusks *Coretus corneus*, *Galba truncatula* and *Galba palustris*. Among the terrestrial species, *Helix lucorum* was quite resistant to infestation, while the species of *Agriolimax* were completely resistant. The freshwater mollusks *Limnea stagnalis* and *Radix auricularia* were relatively resistant to infestation.

From these observations it was adduced that small-sized mollusks are more prone to nematodal infestation. A smaller proportion of mollusks are infected as they grow larger. Thus *Helix lucorum*, which

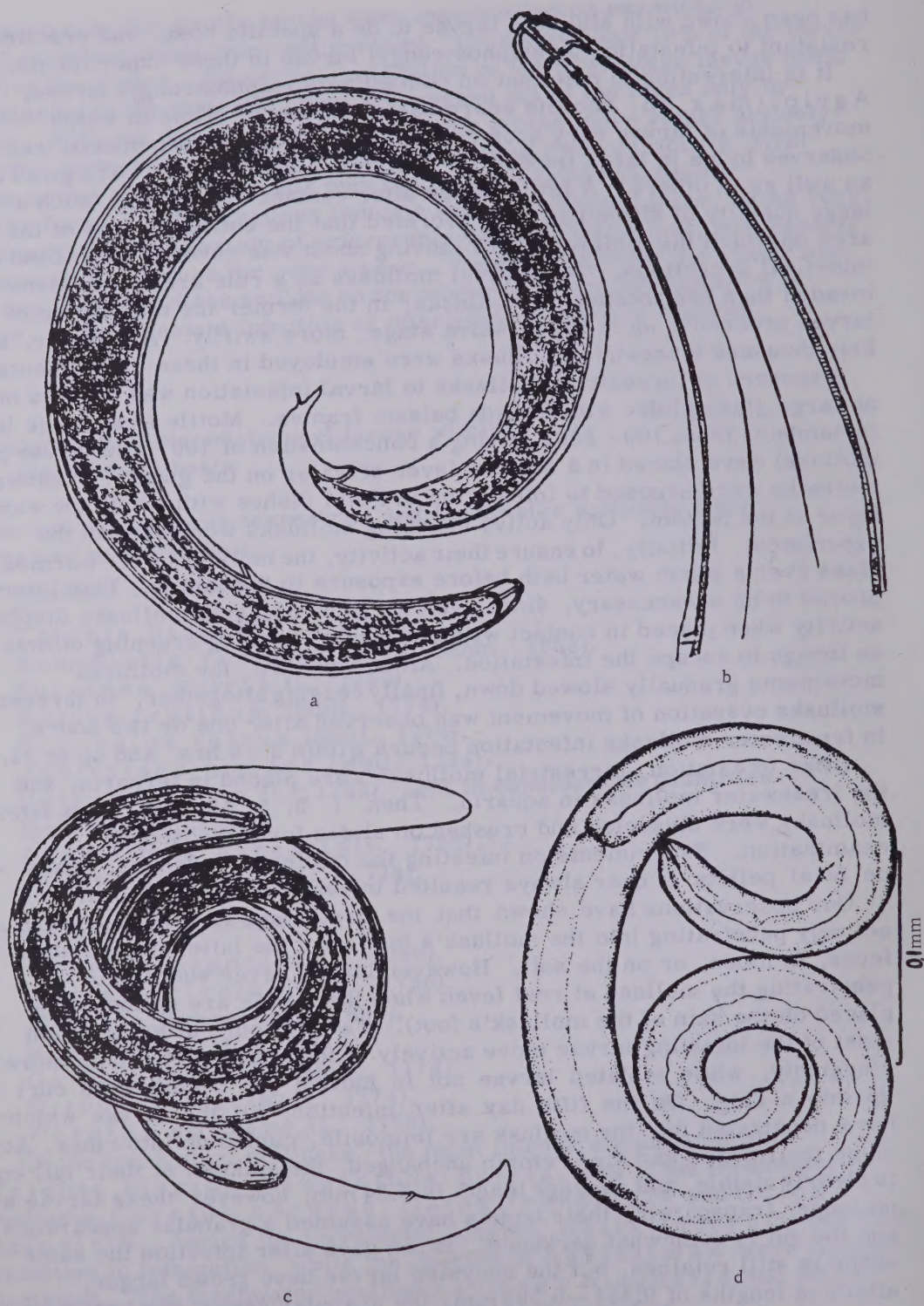
has been shown with Müller's larvae to be a specific host, was practically resistant to infestation by elaphostrongyl larvae in these experiments.

It is interesting to note that on contact with elaphostrongyl larvae, *Agriolimax* sp. secrete enormous quantities of slime in which movements of larvae very soon cease. An analogous phenomenon was observed by us in large freshwater mollusks like *Limnea stagnalis*, as well as in others. A few minutes after contact with larvae, such a large quantity of slime had been secreted that the entire surface of the area on which the mollusks were moving about was covered with it and with intestinal secretions. Terrestrial mollusks as a rule are more intensively invaded than are freshwater mollusks; in the former the maturation of the larvae proceeds, up to the invasive stage, more swiftly. Altogether, some four thousand terrestrial mollusks were employed in these experiments.

Exposure of terrestrial mollusks to larval infestation was carried out on large glass slides with Canada balsam frames. Motile first-stage larvae in numbers from 100—6000 (giving a concentration of 100—200 larvae per mollusk) were placed in a shallow layer of water on the glass. Freshwater mollusks were exposed to infestation in Petri dishes with a shallow water layer at the bottom. Only active creeping mollusks were used in the experiment. Initially, to ensure their activity, the mollusks were warmed in glass over a warm water bath before exposure to the larvae. This later proved to be unnecessary, since even the most sluggish mollusks displayed activity when placed in contact with the larvae, making creeping efforts as though to escape the infestation. After exposure, the mollusks' movements gradually slowed down, finally ceasing altogether. In terrestrial mollusks cessation of movement was observed after one or two hours. In freshwater mollusks infestation occurs within 3—6 hrs, and up to 24.

After infestation, terrestrial mollusks were placed in terraria, and the freshwater mollusks in aquaria. Then, 1, 3, 5, 10, etc., days later, mollusks were dissected and crushed on slides for microscopic examination. Experiments on infesting the mollusks on leaves, grass, or on fecal pellets of deer always resulted in very feeble infections.

Our observations have shown that the first-stage larvae succeed in actively penetrating into the mollusk's foot when the latter creeps about in feces, in moss, or on the soil. However larvae never succeed in penetrating the mollusk at rest (even when the larvae are deliberately placed on the skin of the mollusk's foot). Twenty hours after infection most of the infesting larvae move actively in the host's foot, some more sluggishly, while isolated larvae not in motion are observed to curl up into a ring. On the fifth day after infection, all the larvae which have penetrated into the mollusk are immobile, curled up into rings. At this stage their shape and size remain unchanged, the spikelet at their tail end is clearly visible, and average length is 0.34 mm; however these larvae are no longer transparent, their bodies have assumed a granular appearance, and the gut is somewhat darkened. Seven days after infection the same shape is still retained, but the encysted larvae have grown larger, attaining lengths of 0.384—0.393 mm; the granular aspect has become more pronounced, and the gut has become still darker. Ten days after infection the larvae are 0.456—0.489 mm long. The gut has become almost black, the body granular, and the larvae appear as immobile black rings.



Encysted larvae of *E. rangiferi*; a—at 15 days; b—head of 15-day larva; c—at 25 days; d—at 45 days.

Twelve to thirteen days after infection the molt commences and the light-colored, sheathlike skin becomes particularly clearly discernible in the regions of the head and tail. The exfoliation of the skin along the entire length of the larva's body is well discerned after the larva is immersed for a brief period in water. After 15 days, the exfoliation of the skin from the encysted larva is considerable, especially at the tail end. The tail is very motile and bends about inside the loose skin. The spikelet remains on the skin while the tail end is smooth and pointed. At this stage the larva is dark and granular and the gut black; the larva's length, not including the skin, is 0.759—0.798 mm (see a, b in Figure).

After 20 days, the outer skin enclosing the encysted larva appears looser still, and the length of the larva itself reaches up to 0.816 mm. The larva becomes less granular in appearance and the gut grows lighter in color. After 25 days, larvae still exhibit very marked exfoliation of the skin, but in some of them the skin clings tightly to the larva's body and is hardly visible. The larva becomes transparent and its gut appears gray in color. The broad tail end tapers markedly on the dorsal side near the pointed tip.

After 30 days, the larva is practically devoid of granularity, and while the contours of the gullet, gut and the excretory duct are visible, the gut is no longer dark in color, so that the larva has become quite transparent and almost invisible under a magnifying glass. It is tightly enveloped by the skin. Its length (as that of a 25-day larva) is 0.93—0.948 mm. After 35 days the larva is similar morphologically and in size to the 30-day larva; the amplitude of fluctuations in the length of body and in dimensions of the organs remains like that of the 25-day larvae, viz., from 0.83—0.948 mm in length (see c in Figure).

Larvae examined by us at 40, 45, 50, 55, 60, 70 and 75 days did not differ from larvae examined after the 27th day; the length of these larvae fluctuated between 0.858 and 1.014 mm.

It follows, then, that the invasive larval stage is reached 27—35 days after infestation of the intermediate mollusk host.

Invasive larvae have an average length of 0.933 mm, and average breadth of 0.039 mm; the length of the gullet is 0.342 mm and its width 0.024 mm. The excretory aperture is 0.147 mm distant from the head end, and the anal aperture 0.051 mm from the tail end. The invasive larva is covered by a light-colored skin which clings tightly to the body and is hardly distinguishable. The tail end is short and broad, abruptly tapering towards the sharp-pointed tip on the dorsal side. It is devoid of the supplemental spikelet. The invasive larva lies curled up into a compact light-colored ring and never encysts (see d in Figure).

Invasive-stage larvae in a mollusk's foot sometimes number several hundred. They evidently live within the mollusk during its entire lifetime, even persisting in the dead mollusk for a long period. Live, motile, invasive larvae were still detected by us in the mollusk's body six months after the initial infection. As long as a single drop of moisture is there, they remain in the mollusk's body after its death. The rotting of the dead mollusk's body does not kill the invader larvae.

From the 10th day after infestation of the mollusk's foot, larval development proceeds erratically. The larger the number of encysted larvae in the host's tissue, the more varied are the stages visible. Even 60—65 days following infection, larvae detected in the mollusk range from

10-day stages, dark and granular, to the light-colored transparent invasive larvae; however, the latter are more prevalent. Seventy-five days after infestation of the mollusk host, all the larvae are of the invasive type.

When mollusks become infected in winter, even under indoor conditions, the development of larvae to the invasive stage takes several months longer. After penetration into the mollusk's foot the larvae fall into a latent state and remain quiescent in the host's tissues during all stages. When such a mollusk is crushed, and the larvae emerge into moist conditions, they begin to move energetically with snakelike motions. The invasive larvae are particularly motile.

Before molting, the motility of larvae is poor. In moist conditions (in Petri dishes) invasive larvae squeezed out of a mollusk's foot, or in the foot itself, remain alive up to 35 days or more. We have never observed the actual emergence of invasive larvae from the intermediate host to the external medium. When left in the open air for a whole winter, in special plywood boxes containing turf and leaves, 4% of the invasive larvae survived. However, larvae in various stages of development in a mollusk's foot, whether motile or not, proved capable of active motion on being squeezed out of the tissue.

The elaphostrongylosis infection of deer, then, evidently only occurs when infected mollusks are swallowed together with grass, moss, leaves, or other foods. Deer are liable to infection all the year round if their food contains mollusks, even dead. Since mollusk mortality is high in winter, most mass infections probably take place in autumn, when elaphostrongyl larvae infesting the new generation of mollusks rapidly develop from the first stage to the invasive stage.

Elaphostrongyl development within the definitive host

Invasive larvae obtained from the foot tissue of terrestrial and freshwater mollusks were fed to 2—5-month-old deer. The animals were kept free from contact with any possible intermediate hosts. Three to five months later the feces of all experimental animals contained larvae in the first stage of development. At first (after 3 months) only solitary larvae were detected, excreted occasionally at long intervals; after 4 to 5 months, excrement contained massive numbers of larvae. In January to March, each sample yielded from 800 to 4000 and more larvae. In deer born during the year of the experiment, and infected spontaneously, the first appearance of solitary larvae occurred as a rule when deer were 8 to 9 months old, in December, January or later. In 4—4.5-month-old deer, isolated larvae were found only in some herds, and then in insignificant numbers (5—12%).

By the middle of May the extent of invasion of young animals reaches 80%, but the intensity of infection is still insignificant. Examination of excrement samples gave counts of from a few solitary larvae to tens of larvae per sample. As the deer grow, both the intensity and extent of incidence of infection increase: in some herds 100% of the adult animals are infested, and larvae in samples number up to several thousand. Maximum quantities of larvae in adult deer are detected in late

autumn, and in 1.5—2-year-old animals in March and April. Patterns in the levels of larval excretion have not been observed.

We have not made any special observations to ascertain the length of the elaphostrongyl's life with the host (deer) organism. Although systematic examinations of the same infected animals were carried out for a period of 6 years, complete disappearance of larvae from their feces has never been observed. This may be taken as indication of elaphostrongyls' longevity, or else of the constant reinfection of deer with elaphostrongylosis due to the absence of specific immunity to this nematode.

In experimental infection of 2 to 5-month-old deer, emaciation, retarded general growth, retarded growth and molting of the antlers were observed. Such symptoms could be seen (but more weakly) as early as one month after infection. By the time 8 to 10 months had elapsed this difference between infected and control hosts had gradually disappeared. When deer were fed up to 200 larvae no change in their behavior could be observed, whereas intake of 300 or more larvae was followed 24 hours later by slight depression and the refusal to take food; but these symptoms soon passed. When a 5-month-old deer was given 620 invasive larvae with his food, 24 hours later he rejected food, his breathing became heavy and halting, and moods of depression were followed by excited states. Another young deer, 2 months old, was fed 100 larvae and died in 2 months. On dissection, 34 adult elaphostrongyls were detected under the pia mater and in the convolutions of the cerebral hemispheres; there was slight edema of the brain with punctate hemorrhage in the region of the cerebral hemispheres. Only 34% of the larvae, then, had found their way into the young deer's brain; the rest either perished or penetrated other organs (in this case, muscles were not examined for elaphostrongyls).

We dissected another 5 experimental animals aged 7 to 9 months. All had sexually mature elaphostrongyls, in larger or smaller numbers, under the fascia of the muscles. Only in one animal 2 solitary elaphostrongyls were found in the brain (one under the dura mater and the other under the pia mater). Elaphostrongylosis infection, then, occurred in the muscles in 100% of cases, and in the brain in 20 to 33.3% of cases.

In the five experimental deer, elaphostrongyls were detected in the organs in the following percentages: in intercostal muscles (14.3—46.7%), in the muscles of the left hind limb (25%), in the muscles of the neck (23—25%), in the muscles of the right forelimb (14.3—15.3%), in the muscles of the right hind limb (10.7—15.9%), in the brain (7.5%), and under the peritoneum (2%).

In the nematodes' locales, under the muscle fascia, punctate hemorrhages are occasionally observed. The lungs are almost invariably covered with small hemorrhages and are more or less edemic and hyperemic. Larvae of elaphostrongyls are detected in the lungs, the blood, and washings of the pericardium and trachea.

Thus, our observations showed that young animals usually contract infection at the age of 4 to 5 months, the parasites attaining sexual maturity within 4 months.

To check upon host specificity of *E. rangiferi*, we fed invasive larvae to a guinea pig and to two lambs. The former was given 400 larvae from the foot of *Coretus corneus* mollusks, with an eye-dropper. The guinea pig died suddenly after 5 days. No larvae were detected in its tissues and organs.

The two lambs received invasive larvae obtained from the feet of *Trichia hispida* in bread boluses; lamb no. 1—1050, and lamb no. 2—350 larvae. On the fifth day lamb no. 1 could hardly stand; pushing its head against a box, it moaned and clotted blood collected around its nose. All these symptoms passed within 24 hours, but on the 13th day after infection the lamb succumbed. Although no obvious symptoms were observed in lamb no. 2, it died on the 9th day after infection.

Dissection of the body of lamb no. 1 revealed foamy serous liquid in the nasal cavity and trachea, a tumbler-full of serous liquid in the thoracic cavity, and a spoonful of this liquid in the pericardial sac. Also edema of the lungs, serous pneumonia in the anterior lobes of the lung, grayish nodules on the lung's edges, hemorrhages of striped appearance in the gullet, and pigmented and enlarged mesentery glands. Larvae were not detected either in the brain or in other organs.

Similar changes, but less markedly expressed, were found in the body of lamb no. 2. The control lamb remained alive.

The possibility of cross infections is undoubtedly a problem that requires examination in an extensive experiment.

This research has shed some light on the prospects for combating elaphostrongylosis in deer. In view of the annual, extremely massive and virulent infestation of pastures with excreta of diseased deer, as well as the findings that larvae retain the capacity to survive up to two years on pastures, even under the most unfavorable conditions, and that a great variety of possible intermediate hosts exist, measures for combating this disease will be fraught with considerable difficulties.

The great survival capacity of the larvae coupled with the specific conditions of deer maintenance, render practically impossible the implementation of measures against this worm by cleansing of pastures of intermediate hosts and prophylactic measures to prevent infection of the deer. In our view the best line of attack against this disease lies in the elaboration of methods for prophylaxis of the deer and sterilization of the initial invasive factor—the first-stage larvae—both in the deer itself, and in the animal's feces. Stringent pasture management procedure, with three-year rotation of pasturage lots, to prevent the return of deer to pastures already utilized during the current year, may also improve sanitation of pastures.

Conclusions

1. First-stage larvae are very resistant to low temperature, direct solar radiation, single and repeated drying and freezing. These free-living first-stage larvae are capable of survival in natural conditions for approximately two years. Surviving both the dry season and winter in most unfavorable external conditions, they accumulate in large quantities on pastures and in water.

2. First-stage larvae do not survive heat treatment above 50°C.
3. Water appears to act as a preservative for first-stage larvae at any season of the year. Under 8 cm of water larvae live longer than under 3 cm.
4. The most susceptible intermediate hosts among freshwater and terrestrial mollusks are *Trichia hispida* (L., 1758), *Succinea putris* (L., 1758), *Coretus corneus* (L., 1758), and species of the genus *Galba*. *Agriolimax* sp. are completely immune to infestation.
5. In the summer larvae in the body of the intermediate host reach the invasive stage after 27 to 30 days; in the winter or under other unfavorable conditions, development is retarded and takes at least 60 days. Invasive larvae do not spontaneously leave their intermediate hosts.
6. Infection of deer is only possible when infested mollusks are eaten by the deer together with the fodder. Mass infections occur in autumn by means of young infested mollusks. As a rule, young deer are infected at the age of 4 to 5 months, more rarely during the first month of life.
7. *E. rangiferi* in the deer reaches sexual maturity in 3 to 4 months.
8. Sexually mature elaphostrongyls concentrate predominantly in the muscle (100%), and more rarely in the brain (20—33.3%). Most violently attacked are the intercostal muscles and the muscles of the neck and hind limbs.
9. The span of *E. rangiferi*'s life in the organism of deer, and also the possibility of infection of other ruminants must be ascertained.

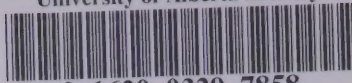
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* [Russian "panty" refers to the soft core of young antlers of certain species of European and Oriental deer. Pantocrine, extracted from the "panty," is extensively used in Russia and the Far East as a medicament and tonic.]

** [NKSKh—Narodnyi Komissariat Sovkhozov (People's Commissariat of Sovkhozes)]



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